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滇东北昭通早泥盆世盔甲鱼类一新属种[1)]

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关键词 云南昭通 早泥盆世 盔甲鱼类 昭通鱼科

内 容 提 要

本文记述了在滇东北昭通早泥盆世 Pragian 期坡松冲组中发现的盔甲鱼类一新属种,让氏昭通鱼 (*Zhaotongaspis janvieri* gen. et sp. nov.),该属至少具有 31 对鳃穴,这是迄今为止记述过无颌类中的最高数目。基于昭通标本,建立了盔甲鱼类一新科,昭通鱼科 (Zhaotongaspidae),该科隶属于多鳃鱼目。箭甲鱼属 (*Antiquisagittaspis*) 是新科的可能成员。文章认为,昭通鱼科与都匀鱼科 (Duyunaspidae) 有较近的亲缘关系。

1991年5月中国科学院古脊椎动物与古人类研究所早期脊椎动物课题组赴云南昭通采集化石,在昭通市东北约10公里的箐门附近下泥盆统坡松冲组(Pragian期)中发现了许多早期脊椎动物化石(图1),有盔甲鱼类、盾皮鱼类及总鳍鱼类。现将盔甲鱼类一新属种让氏昭通鱼 (*Zhaotongaspis janvieri*) 记述如下。该盔甲鱼至少具有31对鳃穴,有可能达到35—40对,这是迄今为止记述过无颌类中鳃穴的最高数目。这有助于对盔甲鱼类鳃穴构造的探讨。根据昭通标本建立了盔甲鱼类一新科,昭通鱼科(Zhaotongaspidae),该科可能包括箭甲鱼属 (*Antiquisagittaspis*),与都匀鱼科之间具有许多相似特征,有较近亲缘关系,后者则以其内部解剖构造保存之精美而著称。

盔甲鱼亚纲 Galeaspida Tarlo, 1967
多鳃鱼目 Polybranchiaspiformes Liu, 1965
昭通鱼科(新科) Zhaotongaspidae fam. nov.

科的特征 盔甲鱼类。具有31对以上紧密排列的鳃穴,鳃穴向后几乎达头甲后缘。角发育,紧接眶孔之后并向后侧方伸展。角后的头甲部分长。中背孔大,横椭圆形或圆形。眶孔侧位。

模式属 昭通鱼属 (*Zhaotongaspis* gen. nov.)

比较 箭甲鱼属 (*Antiquisagittaspis* 刘玉海,1985)可能属于该新科。箭甲鱼属具有一对发育的角,相对位置与形态同于昭通鱼属。此外,箭甲鱼属具有一大的中背孔及侧位眶孔,但由于不清楚箭甲鱼属的鳃穴数目,而鳃穴数目是新科的一个重要鉴定特征,因此这里将箭甲鱼属作为新科的一个可能成员。

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就角的形态而言，新科接近于华南鱼目，不同之处在于前者位于角后的头甲部分相当长。昭通鱼属的角是向后侧方向伸展，而华南鱼目的角是侧向伸展。它们之间在鳃穴数目上也有区别。

昭通鱼属以其大的中背孔和众多数目鳃穴接近于都匀鱼科，区别在于后者眶孔背位，并且角已缺失。

昭通鱼属(新属) *Zhaotongaspis* gen, nov.

特征 昭通鱼类。中背孔非常大，横椭圆形；角内缘具有12～20个棘状小刺。

模式种 让氏昭通鱼(新种) *Zhaotongaspis janvieri* gen. et sp. nov.

词源 从产地，昭通 Zhaotong, aspis (Gr.) 盾甲。

比较 新属与箭甲鱼属的区别主要在中背孔的形状，后者中背孔为圆形，而新属中背孔则为横椭圆形。其它特征如角内缘具小刺及鳃穴的数目，由于在箭甲鱼属的标本上没有保存，因此不能作深入比较。

让氏昭通鱼(新种) *Zhaotongaspis janvieri* sp. nov.

(图 2—5，图版 I—II)

种的特征 同属征(唯一的种)

正型标本 V9759. 1，一件较完整的头甲。

其它材料 V9759. 2—3，不完整的头甲。

词源 赠 Ph. Janvier (让维埃)博士。

产地与层位 云南昭通箐门，早泥盆世，Pragian 期坡松冲组。

描述与讨论 见英文部分。

(1994年3月16日收稿)

ZHAOTONGASPIS JANVIERI GEN. ET SP. NOV., A GALEASPID FROM EARLY DEVONIAN OF ZHAOTONG, NORTHEASTERN YUNNAN

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Key words Zhaotong; Early Devonian; galeaspids; new taxon;

Abstract

A new galeaspid, *Zhaotongaspis janvieri* (gen. et sp. nov.), from the Posongchong Formation (Early Devonian, Pragian) of Zhaotong, northeastern

Yunnan, China is described. This genus is characterized by at least 31 pairs of branchial fossae, which is the highest number ever recorded in agnathans. Its overall morphology is suggestive of both the Polybranchiaspiformes and Huananaspiformes. A new galeaspid family, Zhaotongaspidae (fam. nov.), is erected on the basis of the Zhaotong material, and suggested that *Antiquisagittaspis* is a possible member of the new family. It is also proposed that the Zhaotongaspidae might have the close affinity with the Duyunaspidae.

The first early vertebrate described from the Devonian of Zhaotong, northeastern Yunnan (Fig. 1), was the galeaspid *Sanqiaspis zhaotongensis* (Liu, 1975). The fish-bearing horizon was thought to belong to the "Cuifengshan Formation", that is, Pragian in age, in comparison with the type locality of this formation in the Qujing district, Yunnan. Liao *et al.* (1978) considered that it would be more appro-

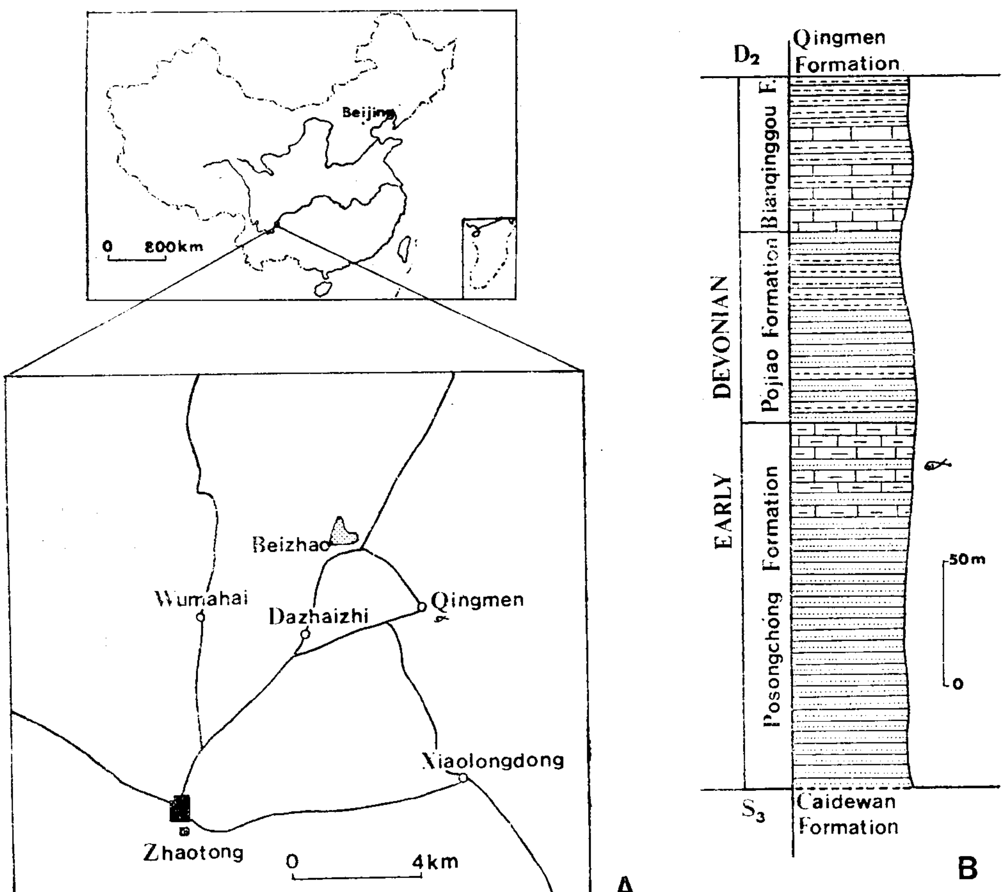


Fig. 1 A. Locality map, showing the site (the sign of a fish in the figure) where the material under description was collected; B. Synthetic log of the Early Devonian in Zhaotong area, Northeastern Yunnan, China.

图 1　A. 化石点平面图；　B. 云南昭通地区下泥盆统综合柱状图

priate to name the horizon as the Posongchong Formation, since it has the same lithology and fauna as the Posongchong Formation in the Wenshan district, Yunnan. This suggestion is followed in this paper (Fig. 1B). Pan and Wang (1981)described a second galeaspid, *Qingmenaspis microculus*, from the same site. In May 1991, a field team from the Institute of Vertebrate Paleontology and Paleoanthropology (IVPP) went to investigate the original site and made a new collection. In this collection, there is a galeaspid which possesses at least 31 pairs of branchial fossae, that is, the highest number ever recorded in agnathans. It bears some similarities with duyunolepids, which are well known for the preservation of their internal anatomy (P'an *et al.*, 1978; Halstead,1979). By now, four species of galeaspids occur in Zhaotong, i.e. *Sanqiaspis zhaotongensis, Qingmenaspis microculus, Lungmenshanaspis kiangyouensis* (Wang *et al.*, in prep.) and *Zhaotongaspis janvieri* (gen. et sp. nov.). The fish fauna also includes a porolepiform and an antiarch (Wang *et al.*, in prep.), which suggests a high diversity.

SYSTEMATIC PALEONTOLOGY

Subclass GaleaspidaTarlo, 1967

Order Polybranchiaspiformes Liu, 1965

Family Zhaotongaspidae fam. nov.

Diagnosis Galeaspid with numerous (31 or more) pairs of closely set branchial fossae extending posteriorly almost to the posterior extremity of the head-shield; cornua well developed, arising just behind the orbits, and projecting posterolaterally; the portion of shield behind the cornua fairly long; median dorsal opening large, oval (transversally elongated) or rounded in shape; orbits laterally placed.

Type genus *Zhaotongaspis* gen. nov.

Remarks It is possible that *Antiquisagittaspis cornuta* (Liu, 1985) can be assigned to this new family. *Antiquisagittaspis* possesses a pair of lateral cornua which have the same relative position as those of *Zhaotongaspis*. It also has the large median dorsal opening and laterally placed orbits. But nothing is known of the number of branchial fossae which is a crucial character of this new family. Therefore we consider *Antiquisagittaspis* only as a possible member of the Zhaotongaspidae.

The pattern of the sensory-line canal system of this family remains poorly known. From the available information, it seems to be of the polybranchiaspid type *sensu* Liu (1986).

As to the shape of cornua, *Zhaotongaspis*, as well as *Antiquisagittaspis*, is suggestive of huananaspiforms, such as *Huananaspis* (Liu, 1973, 1975), *Asiaspis* and *Lungmenshanaspis*(P'an *et al.*, 1975). But it differs from the latter by the long head-shield portion extending behind the cornua. Also, the cornua of *Zhaotongaspis* are posterolaterally directed, while those of huananaspiforms are projecting laterally. Moreover, *Zhaotongaspis* has more than 31 pairs of branchial fossae, which is the highest number among vertebrates.

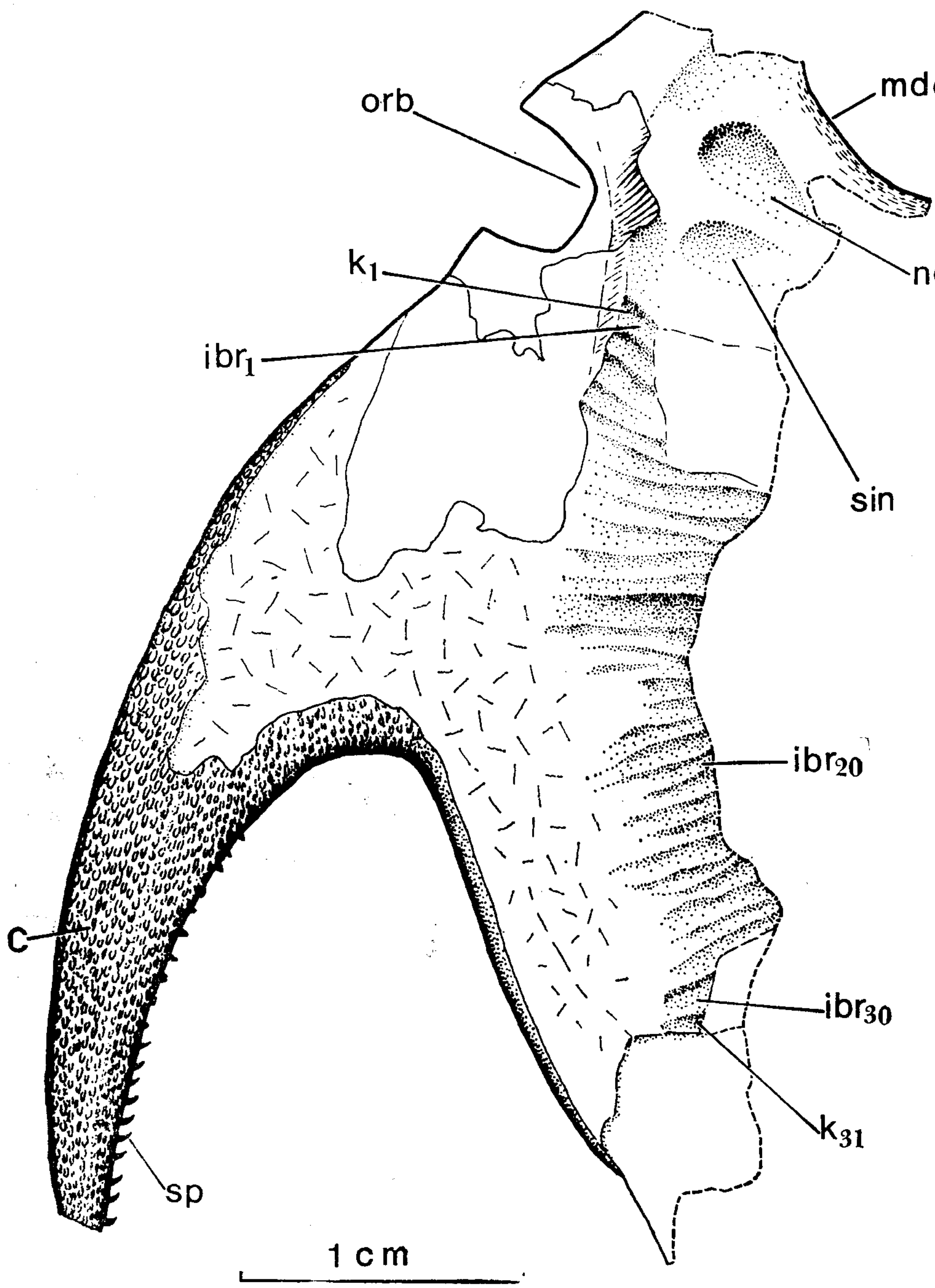


Fig. 2 *Zhaotongaspis janvieri* gen. et sp. nov. Lower Devonian (Pragian), Posongchong Formation, Qingmen, Zhaotong, Yunnan. The sketch of the holotype (V9759. 1).

图 2　让氏昭通鱼正型标本素描图

Regarding the long head-shield portion behind the cornua, *Zhaotongaspis* resembles somewhat *Nanpanaspis* (Liu, 1965; 1975). However, the branchial chamber region in *Nanpanaspis* is quite different from that of *Zhaotongaspis*. *Nanpanaspis*

has a long head-shield portion behind branchial fossae which are few in number. Moreover, *Nanpanaspis* has a longitudinal oval median dorsal opening and dorsally placed orbits.

Zhaotongaspis resembles the Duyunaspidae (P'an et Wang, 1978) by its large median dorsal opening and numerous branchial fossae. However, the latter differ by the lack of cornua.

Genus *Zhaotongaspis* gen. nov.

Diagnosis As for the type species, by monotype.

Type species *Zhaotongaspis janvieri* gen. et sp. nov.

Etymology After the town of Zhaotong, Yunnan, China, and *aspis* (Gr.), shield.

Remarks It is possible that *Antiquisagittaspis* is a member of the Zhaotongaspidae as stated above. *Zhaotongaspis* differs from *Antiquisagittaspis* mainly by the

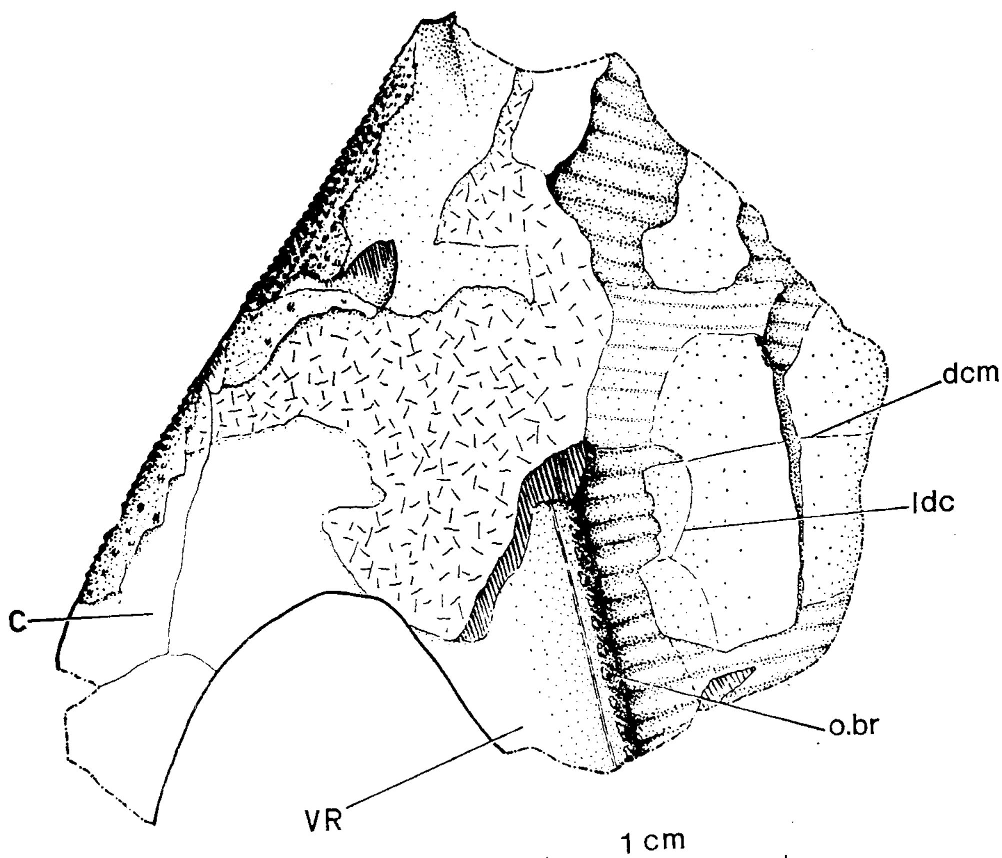


Fig. 3 *Zhaotongaspis janvieri* gen. et sp. nov. Lower Devonian (Pragian), Posongchong Formation, Qingmen, Zhaotong, Yunnan. The sketch of V9759.3.

图 3 让氏昭通鱼 V9759.3 号标本素描图

shape of the median dorsal opening. The median dorsal opening of *Antiquisagittaspis* is rounded in shape whereas that of the new genus is transverse and oval in shape.

Zhaotongaspis janvieri gen. et sp. nov.

(Figs. 2—5; Pl. I—II)

Diagnosis Zhaotongaspid with a very large transverse, oval median dorsal opening; the inner margin of the cornua is armed with 12—20 spine-shaped denticles.

Holotype A left side of the head-shield (V9759. 1, Fig. 2, Pl I—2).

Type locality and horizon Qingmen, Zhaotong, Yunnan, Posongchong Formation, Early Devonian, Pragian.

Etymology After Dr. Philippe Janvier

Referred material V9759.2—3.

Description All three specimens are imcompletely preserved. The holotype

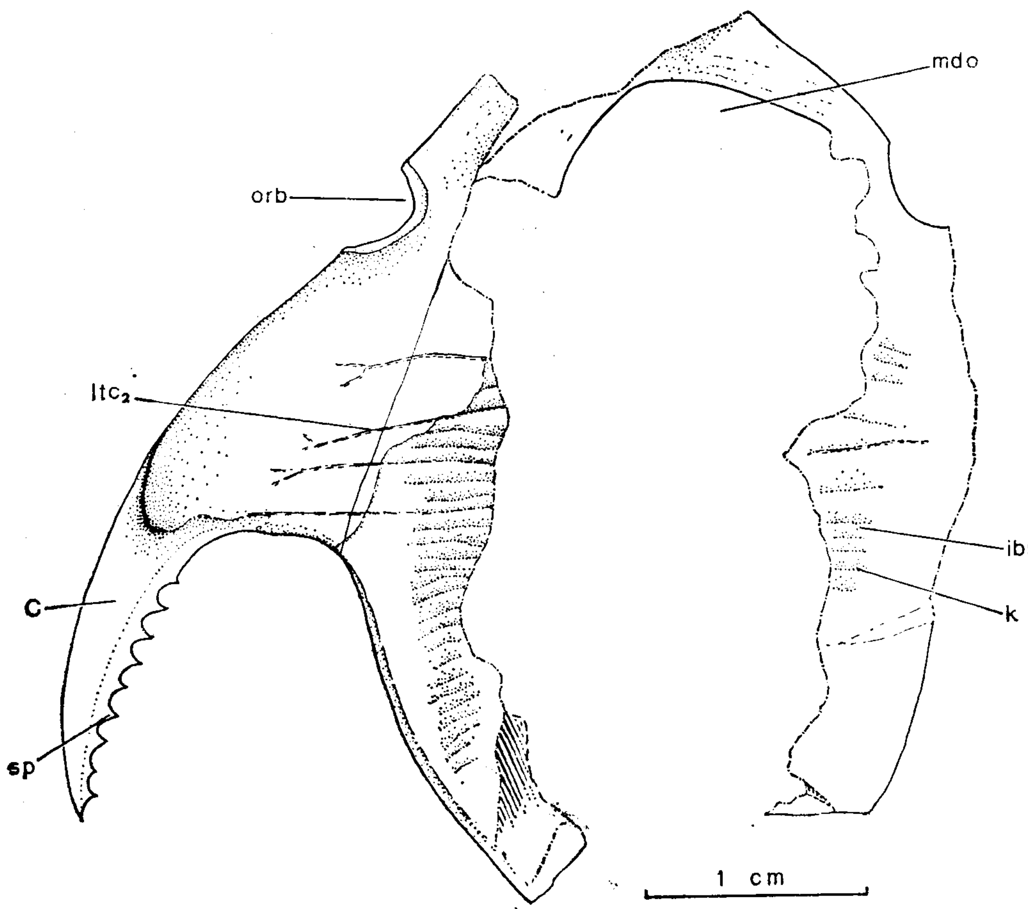
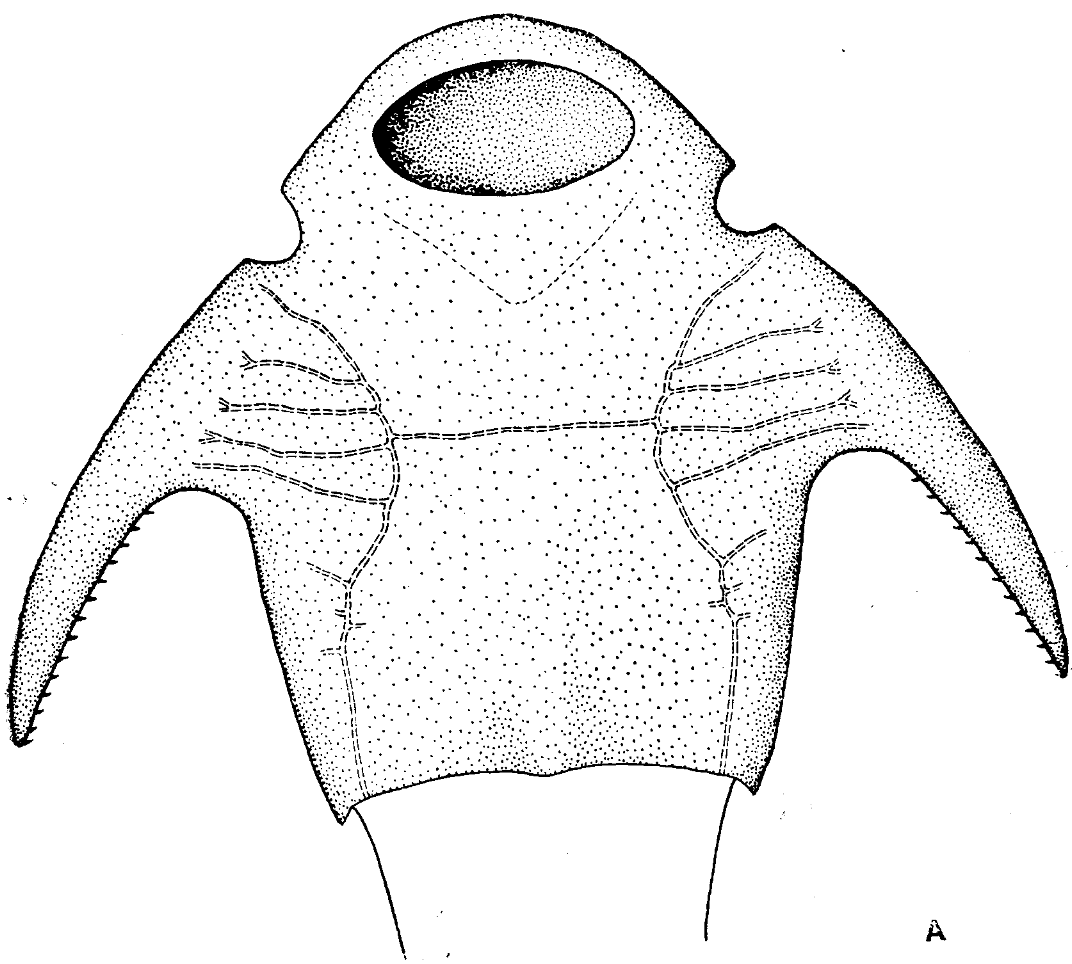


Fig. 4 *Zhaotongaspis janvieri* gen. et sp. nov. Lower Devonian (Pragian), Posongchong Formation, Qingmen, Zhaotong, Yunnan. The sketch of V9759.2.

图 4 让氏昭通鱼 V9759.2 号标本素描图

V9759. 1 (Fig. 2; Pl. I—2) is the left half of the head-shield with the anterior extremity missing. Anteriorly, it shows part of the posterior margin of the median dorsal opening (mdo). The similar preservation is seen in V9759. 3(Fig. 3; Pls. I—3, II—1,2). However, V9759.2 (Fig. 4; Pls. I—1, II—3) shows both halves together, although it has lost the middle portion and the anterior end of the head-shield. On the basis of this specimen, the general morphology (length/width proportion) of the head-shield can be measured, and a reconstruction in dorsal view is made by compiling all specimens (Fig. 5A).

We do not know exactly if this species possessed a rostral process as in huananaspids. A curved rostral margin is provisionally restored in this paper. If *Z. janvieri* did not possess a rostral process, the length of the head-shield could reach 50mm. The orbits (orb) are laterally placed, forming a pair of relatively deep notches along the anterolateral margins of the shield. Immediately behind the orbits arise a pair of cornua (C), which project posterolaterally. The external margin of the cornua prolongs the anterolateral shield margin in front of the orbit. The medial margin of the cornua forms an acute angle (55°—65°) with the posterolateral margin of the



A

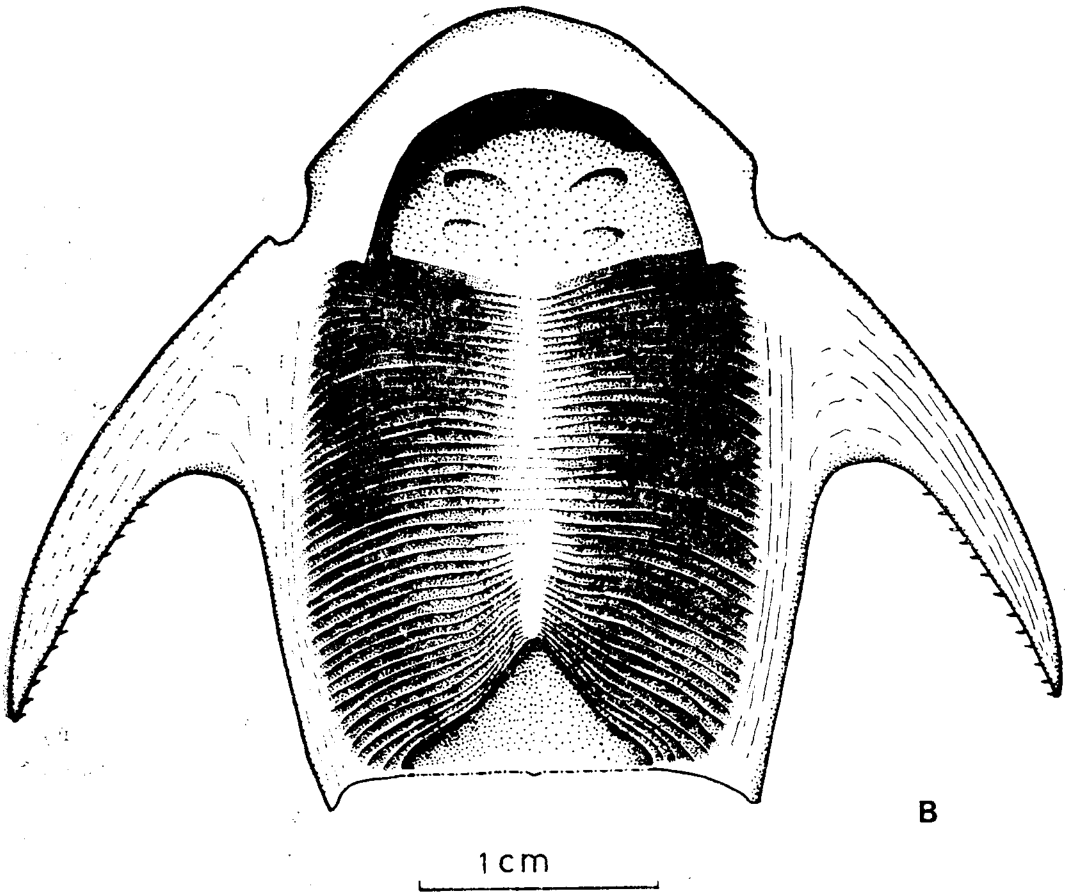


Fig. 5 *Zhaotongaspis janvieri* gen. et sp. nov. Reconstructions of the head-shield in dorsal (A) and ventral (B) views.

图 5 让氏昭通鱼头甲复原图。A. 背视；B. 腹视

shield. Along the medial margin of the cornu, there are 12—20 spine-shaped denticles (sp), as in some of osteostracans, e.g. *Waengsjoeaspis* (Janvier, 1985). But this feature is recorded here for the first time in galeaspids.

The lateral margin of the head-shield behind the base of the cornua is very long, projecting posteriorly and slightly medially. Its posterior end is situated beyond the level of the posterior extremity of the cornua. The length of this part is about half of that of the entire shield.

No complete median dorsal opening is preserved. In addition to the part of the posterior margin of median dorsal opening in the holotype (Fig. 2), V9759.2 (Fig. 4) shows the somewhat distorted anterior margin of this opening, on which is based the restoration proposed here. The median dorsal opening of *Z. janvieri* is very large, oval in shape, transversely elongated, and situated immediately in front of the level of the orbits.

The ornamentation consists of small tubercles (Pl. II—1c). On the surface of the cornua, along their external margin, the tubercles are somewhat elongated in shape (Pl. II—1d), more or less forming ridges as on the spinal plate of arthrodires and petalichthyids. The tubercles around the median dorsal opening show a similar pattern, forming several thin, concentric rings (Pl. I—1b).

The sensory-line canal system is poorly preserved. On the surface of V9759. 3 (Pl. I—3), there are several discontinuous canals or impressions which can be interpreted as sensory-line canals. Some of these canals are also seen in V9759.2 (Fig. 4, Pl. I—1a). The dorsal commissure (dcm)is partly preserved in V9759.3(Fig. 3), and has a relatively posterior position, just in front of the level of the embayment between the cornua and the posterior shield margin. The infraorbital canal (ifc) and the part of lateral dorsal canal (ldc) are seen in V9759. 3. On the lateral side of lateral dorsal canals, six lateral transverse canals are preserved. In V9759.2, there are four subparallel, laterally extending canals with a branching distal end. They belong to the lateral transverse canal system (ltc_{1-4}). No supraorbital canal is preserved. The attempted restoration of the sensory-line canal system in *Z. janvieri* is made here. The sensory-line canal system of *Z. janvieri* seems thus to have the typical polybranchiaspid pattern (Liu, 1986).

The closely set branchial fossae of *Z. janvieri* are quite interesting since they are the most numerous ever observed among vertebrates (Fig. 5B). The oralobranchial chamber occupies most of the head-shield. In V9759. 2, we can observe that the branchial fossae extend posteriorly almost to the posterior extremity of the head-shield. A similar condition occurs in *Duyunolepis*, *Paraduyunaspis*, *Neoduyunaspis* which have up to 24 pairs of branchial fossae. In the holotype, if the foremost ridge represents the postbranchial ridge which is just behind the level of the posterior orbital margin, at least 30 interbranchial ridges (ibr_{1-30}) and 31 branchial fossae (k_{1-31}) could be seen. Since its posterior region is partly eroded, more branchial fossae may have been present. The branchial fossae are best preserved in V9579.4. In this specimen, 27—28 branchial fossae (ridges on the natural mould) and interbranchial ridges (grooves on the natural mould)are clearly seen. Since both its anterior and posterior ends are missing, we suppose that 35 to 40 pairs of fossae would be possibly present in *Z. janvieri*. In the posterior part of V9759.3, on the external mould of the ventral rim (VR) of the head-shield there are 10 small calabash-shaped humps which correspond to the depressions housing the external branchial openings (Pl. II—1a, 1b). Each branchial fossa possesses a branchial opening.

In the holotype, there are two shallow depressions in front of the branchial region. The anterior one (nc) is anteromedial to the orbit, and is possibly the anterolateral part of nasal cavity as in *Changxingaspis gui* (Wang, 1991, fig. 4). The posterior depression is a little smaller and is medial to the orbit. This depression is probably the position of the cavity for the venous sinus of dorsal jugular vein(sin), as in *Duyunolepis* (P'an & Wang, 1978) and *Changxingaspis*.

DISCUSSION

The Galeaspida is a monophyletic group of armoured jawless craniates which

range from the Early Silurian to the Late Devonian, and is distributed endemically in South China, Ningxia, Tarim (Xinjiang, northwestern China) and Vietnam (Halstead, 1979; P'an & Wang, 1981, 1983; Janvier, 1975, 1984; Janvier, Thanh & Phuong, 1993; Liu, 1985, 1986; Pan, 1984; 1992; Wang, 1991; Zhu, 1992). Its synapomorphies include the median dorsal opening in the anterior part of the head-shield and the festooned pattern of the sensory canal system (Zhu, 1992). The monophyly of galeaspids is now well supported, but their in-group relationships are still a most controversial subject, apart from the monophyly of the Eugaleaspiformes (Liu, S.-F., 1986; Zhu, 1992). In our opinion, most of the questions are related to the monophyly of the Polybranchiaspiformes, and especially, the Huananaspiformes. *Zhaotongaspis* shows character of both the Huananaspiformes and Polybranchiaspiformes, which may throw some light on the understanding of this problem. However, the detailed phylogenetic analysis of the group is beyond the scope of the present paper.

The taxon Huananaspiformes was erected by Janvier (1975) and characterized by the rostral process and cornua. As we know now, the rostral process and cornua easily occur by parallelism, and are widely distributed among galeaspids. In the Eugaleaspiformes, *Pterogonaspis* (Zhu, 1992) and *Tridensapis* (Liu S. -F., 1986) have just the same rostral process and cornua as *Huananaspis* (Liu, 1975). *Nanpanaspis* (Liu, 1965, 1975) also has the rostral process and cornua. In the Polybranchiaspiformes, the earliest known galeaspid *Dayongaspis* (Pan & Zeng, 1985) possesses a pair of cornua. Although *Gumuaspis* was originally assigned to the Huananaspidae (Wang & Wang, 1992) because of its well developed rostral process, it is now of little doubt that it should be referred to as the Polybranchiaspiformes, since it has many polybranchiaspid characters except the rostral process. *Zhaotongaspis* is another example. It seems to possess no rostral process as most polybranchiaspiforms, but it bears the cornua like huananaspiforms.

If we leave aside the question of the few galeaspid genera which exhibit the so-called "dorsal fenestra" (Pan, 1992), it is possible to recognize five galeaspid families (Huananaspidae, Sanqiaspidae, Lungmenshanaspidae, Gantarostraspidae and Sanchaspidae) which can be included in the Huananaspiformes by the shape of the cornua and the rostral process. But as addressed above, since these two characters may have appeared or were lost several times in the evolution of galeaspids, they should be considered as the less important characters. We should find other characters to reconstruct the phylogenetic tree.

As stated in the remarks, *Zhaotongaspis* differs greatly from huananaspids, not to speak of sanquiaspids, as it has a long cephalic portion behind the base of cornu. Zhu (1992) had demonstrated that the so-called "corner" of the polybranchiaspid shield is in fact the inner corner of the eugaleaspiform and "huananaspiform" shield. The true cornua are lost in polybranchiaspids. If we did not consider the cornua in *Zhaotongaspis*, we could find it hold many similarities with duyunaspids (P'an & Wang, 1978). Both families possess the large median dorsal opening and the numerous branchial fossae which extend posteriorly almost to the end of the shield. If the inner corners (i. e. the ventrolateral crest of the abdominal division of the

shield) were proved to be lost in *Zhaotongaspis*, the loss of the inner corners would be the third common character of the two taxa. It is suggested here that the Zhaotongaspidae might have close affinity with the Duyunaspidae.

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Abbreviations used in the figures:

C	cornua
dcm	dorsal commissure
ibr_{1-30}	first to thirtieth interbranchial ridge
ldc	lateral dorsal canal
ltc_{1-4}	first to fourth lateral transverse canal
k_{1-31}	first to thirty-first branchial fossa
mdo	median dorsal opening
nc	depression possibly caused by the nasal cavity
o.br	external branchial opening
orb	orbit
sin	depression possibly caused by the cavity for a venous sinus
sp	spine-shaped denticle
VR	ventral rim of the head-shield

Explanation of the plates:

I. *Zhaotongaspis janvieri* gen. et sp. nov.

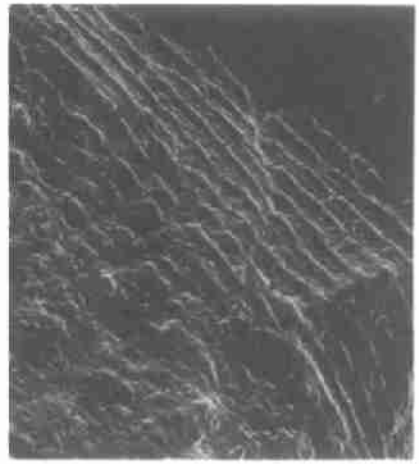
1a, the head-shield (V9759.3), ×3; 1b, SEM photo on the mould of V9759.3(Pl. II—1a) showing the detail of ornaments, ×20; 2, the holotype, a left side of the head-shield (V9759.1), ×3; 3, the head-shield (V9759.2), ×3.

II. *Zhaotongaspis janvieri* gen. et. sp. nov.

1a, the silicon cast of V9759.3 (head-shield), ×3; 1b, SEM photo showing the detail of the external branchial opening, in the same view as the original specimen, ×15; 1c-d, SEM photo showing the detail of tubercular ornaments, in the same view as the original specimen, ×20; 2, the head-shield (V9759.3), ×3; 3, the head-shield (V9759.2), ×3.



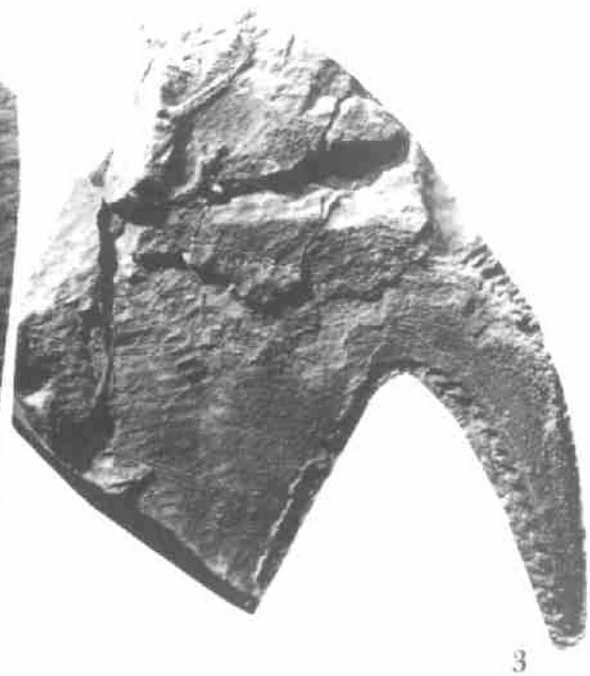
1a



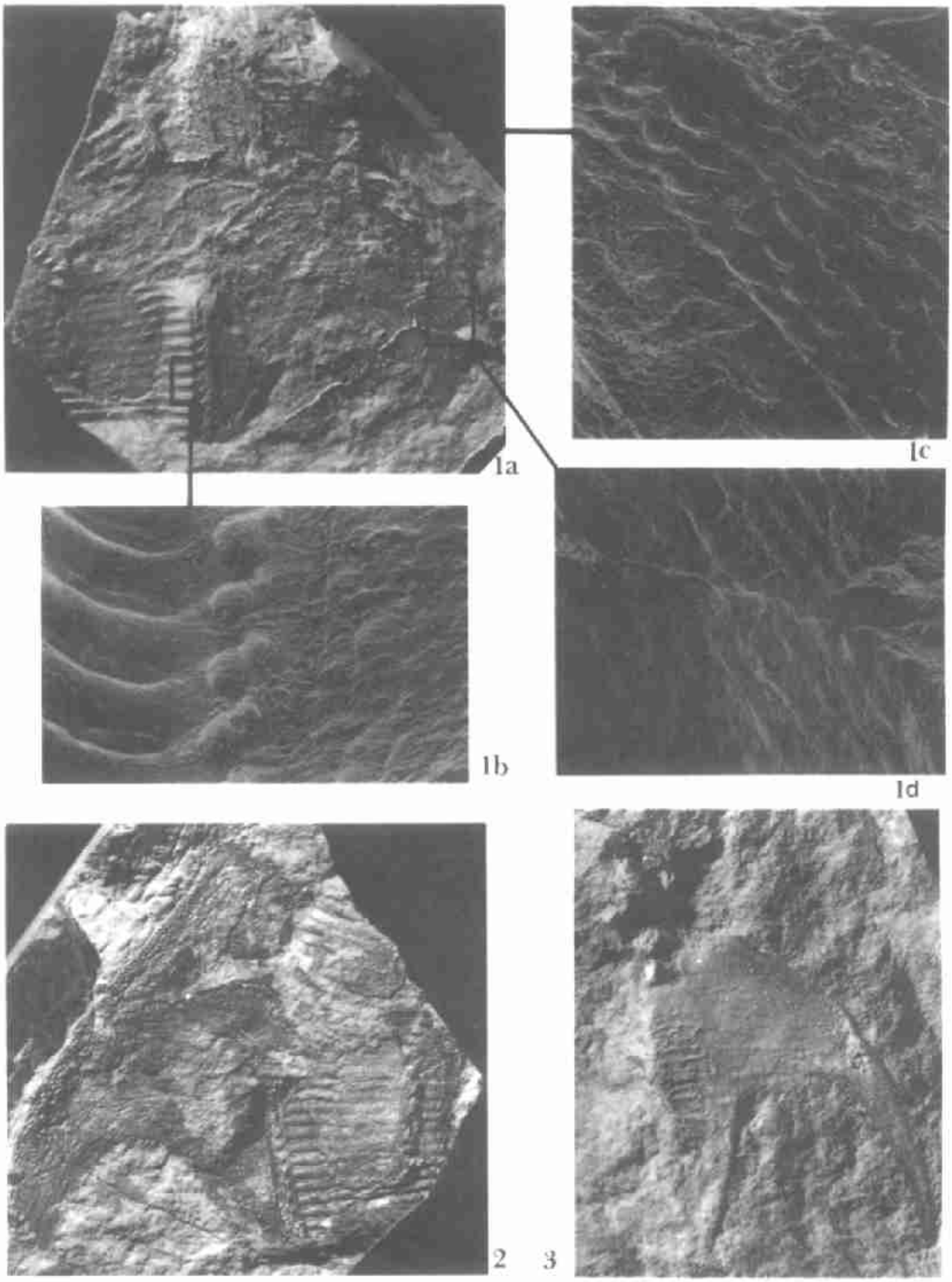
1b



2



3


1a
1b
1c
1d
2
3